à testa dur de 0,4 mm d'épaisseur. Embryon à cotylédons plan-convexes, elliptiques-suborbiculaires, de 10 × 5 mm, charnus, épais de 1,5 mm ; radicule incluse.

TYPE : *Capuron 8875 SF*, arbre de 10 m, de 0,15 m de diamètre, forêt orientale, massif Ambohitsitondroina de Mahalevona, Nord de la presqu'île de Masoala, 200 m, janvier 1954, fl. (holo-, P ; iso-, P).

PARATYPES : *Schatz et al. 1903*, Toamasina, Nosy Mangabe, 5 km de Maroantsetra, Baie d'Antongil, 0-330 m, 14 févr. 1988, fl. (P, TAN) ; *Cheek B1307, ibid.*, févr. 1988, fl. (K, TAN) ; *Schatz, Lowry & Floret 2342, ibid.*, mai 1988, fl. (P) ; *Schatz & Miller 2498, ibid.*, 9 janv. 1989, fr. (K, P, TAN).

Cette espèce est distincte du *Malleastrum mocquerysii* (Tableau 1), également de Nosy Mangabe, qui fleurit en même temps, mais aussi de tous les *Malleastrum* connus, par la longueur des dents du calice et par les bractéoles (caractères peut-être pléiotropiques).

TABLEAU 1 : Caractères distinguant *M. mocquerysii* de *M. sepaliferum*.

	M. mocquerysii	*M. sepaliferum*
FOLIOLES	coriaces jusqu'à 15 cm de longueur avec de nombreuses ponctuations pellucides	chartacées jusqu'à 10 cm de longueur, à ponctuations pellucides rares
PÉDONCULE	3-7 mm de longueur	14-26 mm de longueur
BRACTÉOLE	± 0,5 mm	1,75-5 mm
DENTS DU CALICE	± 0,5 mm	2-5 mm
OVAIRE	3 loges	4-5 loges

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Polysaccharide food-bodies as pollinator rewards in *Exospermum stipitatum* and other *Winteraceae*

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Summary : Petals of several species of *Zygogynum, Bubbia* and *Exospermum* (*Winteraceae*) have cells containing polysaccharide granules that have a dual function in floral biology. Hydrolysis of granules (starch) in floral tissue apparently results in rapid uptake of water with subsequent opening and/or closing of flowers. In addition, granules may function as pollinator rewards for beetles. In one species, *Exospermum stipitatum*, the rose-purple inner surface of the outermost petals characteristically display chewing damage from beetles. Cross sections of this tissue show a "bi-layered" petal, with the innermost cells densely packed with polysaccharide granules. This is the first report of "food-bodies" occurring in the *Winteraceae*.

Résumé : Les pétales de plusieurs espèces de *Zygogynum, Exospermum* et *Bubbia* ont des cellules spécialisées qui contiennent des granules de polysaccharides. Ces granules jouent deux rôles dans la biologie florale de ces espèces. Tout d'abord, il semble que leur hydrolyse contrôle la quantité d'eau dans le tissu des pétales, ce qui provoque l'ouverture et la fermeture des fleurs. De plus, quelques-uns de ces granules sont mangés par les coléoptères qui pollinisent les fleurs. Chez *Exospermum stipitatum*. les surfaces internes rose pourpre des pétales externes sont typiquement mâchés par les coléoptères. Le tissu des pétales de cette espèce est disposé en deux assises, l'intérieure étant remplie de façon compacte de granules de polysaccharides. Cette étude est une des premières portant sur les "food-bodies" chez les *Winteraceae*.

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The *Winteraceae* is an old family of angiosperms with a fossil record extending to the early Cretaceous (Upper Aptian-Lower Albian; WALKER et al., 1983). The 28-30 species of *Winteraceae* (all endemic) on New Caledonia, which is the center of distribution of extant members of the family, are traditionally classified into four genera — *Belliolum, Bubbia, Exospermum* and *Zygogynum* (SMITH, 1943; but see VINK, 1985 for a different opinion).

In *Zygogynum* (CARLQUIST, 1981), *Belliolum* (CARLQUIST, 1983) and *Exospermum* (CARLQUIST, 1982), the rapid opening of flowers is accompanied by a swelling of petals and stamens. CARLQUIST (1982) suggested that the opening of the flowers is a result of uptake of water resulting from the hydrolysis of starch, yielding soluble sugars that change the osmotic

potential. This study describes the presence of polysaccharide granules in the cells of the petals of open flowers for several members of the *Winteraceae*, with special emphasis on their role as food-bodies for pollination in *Exospermum stipitatum* (Baillon) Tieghem ex Pilger. They are also discussed in relation to CARLQUIST's (1982) hypothesis of floral opening in the *Winteraceae*.

MATERIALS AND METHODS

The tree *Exospermum stipitatum* occurs throughout the tropical forest of central and northern New Caledonia (MORAT et al., 1984). Observations were made on, and floral material was collected from, a large population of *E. stipitatum* on Mt. Panié (alt. 325-400 m) in November and December, 1983 and 1986. In this population, most *E. stipitatum* exceeded 20 m in height, but only the lowermost flowers could be collected using a telescoping pole clipper (ca. 8 m in length). A total of 15 flowers from 8 trees were collected; some additional petals were collected from fallen flowers below trees in 1986. A voucher from the population is deposited in the Missouri Botanical Garden (*McPherson 5929*). Insects collected from the flowers were pinned or preserved in 70 % alcohol.

Floral material of *Zygogynum bicolor* Tieghem was collected at 950 m on Plateau de Dogny (*McPherson 5873*) and for *Z. baillonii* Tieghem at 800 m on Mt. Dzumac (*McPherson 5833*). Flowers of *Z. pomiferum* subsp. *pomiferum* (Baillon) Vink were obtained on Mt. Do at 850 m (*Thien 300*), and flowers of *Z. vieillardii* Baillon were collected at 800 m on Prokoméo (*McPherson 6020*). Flowers of *Bubbia pauciflora* (E. G. Baker) Dandy were collected from plants on Mt. Panié at 550 m (*McPherson 5928*). Entire flowers or floral parts were fixed in FAA and/or a fixative of 2 % glutaraldehyde/0.5 m caccodylate, pH 7.0. In the laboratory, subsamples (ca. 2 mm^2) were excised from the specimens and serially dehydrated in a graded series of aqueous ethanols, placed into acetone, and embedded in Spurr's epoxy resin. Alternating thick thin-sections were cut with a diamond knife on a Sorvall Porter-Blum Mt-2 ultramicrotome and dried onto glass slides. The sections were stained with a 1 % aqueous solution of basic fuchsin and/or periodic acid-Schiff's (PAS), following JENSEN (1962).

RESULTS AND DISCUSSION

The flowering season of *E. stipitatum* spans 3-4 months during which individual trees produce a few flowers per day. The floral structure (SAMPSON & TUCKER, 1978) consists of a shallow cup-shaped calyx which encloses the bud during a very early stage in floral development. There are 12-15 petals (usually yellow) in 3-4 tetramerous whorls, with the reflexed outermost rose-purple on the inner surface essentially functioning as sepals (Fig. 1). The numerous stamens have an unordered phyllotaxis (ENDRESS, 1987*a*, 1987*b*); the 4-8 carpels are free, or nearly so, and tightly appressed in the protogynous flowers (SAMPSON & TUCKER, 1978).

The flowering process is similar to that of *Zygogynum* (THIEN, 1980). The flowers are functional for two days, with the female phase (stigmas receptive) exhibited on the first day, and the male phase (anther dehiscence) on the following day. The four outermost petals open

permanently on the first day, while the inner petals remain closed, forming a chamber (Fig. 1). The remaining petals open on the second day. Throughout anthesis, a floral odor is produced (THIEN et al., 1985), which evidently acts as a primary attractant for the insects (PELLMYR, THIEN & BERGSTROM, 1989). Ten of the 15 flowers of *E. stipitatum* collected from the 8 plants contained a total of 26 beetles (*Palontus exospermii, Curculionidae*) inside the closed chamber formed by the inner petals. All the flowers containing beetles displayed chewing damage on parts of the inner surface of the outermost petals (Fig. 1); in two flowers, large portions of the petals were eaten. None of the flowers displayed any damage to the carpels. Sections of floral buds prepared just prior to opening by CARLQUIST (pers. comm.) show petals and stamens rich in starch grains. He assumed that the starch is hydrolyzed yielding sugars in solution, thus affecting the osmotic potential resulting in an inflow of water. It is interesting to note that CARLQUIST (pers. comm.) failed to find starch in the carpels. As noted, no flowers of

Fig. 1. — First day (female phase) flower of **Exospermum stipitatum**. The arrow indicates a portion of the inner surface (the food-body) of an outer petal eaten by beetles (× 2).